THE USE OF INSECT SOUNDS IN TAXONOMY

W. J. Reynolds
Department of Entomology, British Museum (Natural History), Cromwell Road, London, SW7 5BD.

Introduction

The chirps and buzzes made by insects are among the most familiar and evocative sounds of the countryside in summer, but few people who hear them realize the significance of the sounds to the insects making them and listening to them. Take the example of a grasshopper chirping on a grassy bank. It is announcing to the world that it is a male (the females are almost silent) of a particular species and is inviting females of the same species to approach it. The females can recognize the song of their own species and, if they are in the correct physiological state, will approach the male and mating may follow. For the female to be able to recognize the song it must be characteristic of the species and, if it is distinct enough for her to recognize, then we may be able to recognize it too and use it to identify the species. The characters of the song that are species-specific and therefore suitable for such identification normally lie in the temporal patterns and changes in volume.

Not all insect sounds are useful to the taxonomist. The noise a startled insect may make when seized by a predator need not be characteristic of its species in order to be effective; it merely needs to be loud and 'alarming'. Only the sounds used to attract mates are likely to be species-specific.

Sound production

The methods insects use to produce sounds are very varied. Unlike mammals with their larynx and birds with their syrinx, in insects any part of the body that can be scraped against any other is used in at least one group to produce sound. A full review is given by Dumortier (1964), but among the most interesting are a pigmy mole-cricket that rasps its mandibles against its maxillary palps, a reduviid bug that scratches the tip of its rostrum against a ridged area between its front legs, a beetle that rubs a striated part of its front femur against a row of ribs on the side of the prothorax, several groups of ants that scrape part of the petiole against the gaster, and some noctuid moths that produce sound when in flight, using modified areas of the forewings that are presumed to come into contact with suitably modified legs. These are just some of the *frictional* methods of sound production; other methods involve vibration of a membrane or appendage, expulsion of a gas or liquid from a bodily opening, and banging part of the body on the substrate, as, for example, in the death watch beetle.

The cicadas provide the best-known examples of sound production by vibration. At the base of the abdomen they have a pair of tymbals, which are curved areas of cuticle that are made to click in and out like tin lids by muscles on the inside. It is now known that tymbals are also present on most other Homoptera, and that leaf-hoppers, treehoppers and froghoppers also use them for communication; these groups do not, however, have the large abdominal air sacs of the cicada which are tuned to resonate at the natural frequency of vibration of the tymbal and amplify the sound to a level not reached by any other insect.

All the examples mentioned from here onwards will be Orthoptera—the grasshop-pers, crickets and bush-crickets—because that is the group I work on and because Orthoptera are the group in which sounds are most easily used in taxonomy. Many Orthoptera have loud songs that attract mates, they sing from accessible

Modified from a talk presented to the Society on 12 February 1987.

places, and they are fairly easy to catch because they do not usually fly for long distances.

The commonest method of sound production in European grasshoppers consists of rubbing a row of pegs on the inside of each hind femur against a prominent vein on the adjacent forewing. In crickets and bush-crickets the forewings are raised for singing and a row of teeth on one wing is scraped with a plectrum on the other. Grasshoppers usually produce louder sounds during the downstroke of the legs than on the upstroke and, similarly, crickets and bush-crickets normally produce louder sounds during the closing stroke of the wings than the opening one.

Basis for the taxonomic use of song

Although the songs of many species of insects were described over a hundred years ago, they were virtually ignored in taxonomic circles until recently. When taxonomists did start to study the songs, they soon realized that, in many cases, what had been thought to be single species were in fact groups of species with clearly distinct songs. Despite the fact that they are almost or entirely unrecognizable in superficial appearance, there is no doubt that they are different species, because they do not interbreed and often have different behaviour patterns, seasonal cycles and habitat preferences. Usually, once enough specimens with known songs have been collected, it is possible to find subtle and previously unnoticed differences in structure. For example, during the last 30 years many previously unknown species of cricket have been detected in the USA as a result of studies on their songs. Americans have also used songs to elucidate the taxonomy of the periodical cicadas.

By the mid 1960s my colleague Dr D. R. Ragge had convinced the British Museum (Natural History) that a recording laboratory was needed to make and analyse tape recordings of insect songs. Lack of funds caused a delay but work had begun by 1970 and the laboratory came into use in 1973, which was when I joined the staff. There is an outer laboratory, containing most of the equipment, and a sound-proof inner studio where the insect being recorded is placed in a muslin recording cage with a microphone pointing at it, while the recordist sits in the outer laboratory with the tape recorder.

It was decided to concentrate first on the western European fauna, and particularly on the many groups in which there is still taxonomic confusion. There are several reasons for this. First, both field and studio recordings can be made with relative ease and low cost. Second, several groups of European grasshoppers are of economic importance. Third, grasshoppers have recently been found to be excellent subjects for cytogenetic study, and we have been asked by cytologists for taxonomic information at a more advanced level than has yet been reached in these groups. Fourth, grasshoppers and bush-crickets are large, relatively static insects that often occur in dense, well-defined populations, and so lend themselves well to ecological studies, and there have been many comprehensive studies of this kind in western Europe. Fifth, acoustic communication is a good example of Konrad Lorenz's concept of the 'fixed action pattern' and the 'innate releasing mechanism'—a hereditary, predetermined sequence of movements and a system specialized to recognize it. This behaviour is easily triggered and has made Orthoptera a favourite choice for neurophysiologists and neuroethologists, tracing back the origins of behaviour to the central nervous system, sense organs and muscles. These studies have been held up by problems of identification in the more difficult species groups, which have had to be treated as single species. It is therefore felt that working on the taxonomy of the more difficult groups of western European Orthoptera provides a much-needed service to other biologists.

On his first recording trip, to Austria in 1973, Dr Ragge proved that it was possible to make high quality recordings of most Orthoptera in the field; since then we have each made several trips to France, Spain and Italy and altogether have made about 650 recordings which now form the basis of our western European collection.

Equipment and methods

The equipment we use for recording in the field is a Uher tape recorder and an AKG D202 microphone. The microphone has separate low and high frequency sections, and ours has been modified so that the on/off switch is linked only to the low frequency section; with this switched off, most of the unwanted background noises are excluded, leaving the insect sounds unaffected because they are mostly above 1 kHz.

In order to get as loud a recording as possible in relation to the background noise, the microphone should be within a few inches of the subject, which must therefore be approached very carefully so as not to disturb it. The most useful recording is of an isolated male producing 'calling song', i.e. not interacting with any others. If the population is too dense to find an isolated male, one can be caught and taken to a quieter spot and released in the hope that it will start singing. After making a recording it is vital to catch the singer so that it can be examined morphologically. For this reason it has to be permanently associated with the recording.

The tape recorder we use for studio recording is a Nagra IV D, which is also portable, so that it can be used in the field if necessary, but it is twice as heavy as the Uher and so less convenient for field use. The Nagra has built-in filters to reduce the low frequency background noise but an additional filter has been added to ours to cut out frequencies above 20 kHz, i.e. above the range of human hearing. Many bush-cricket and other insect songs contain a lot of sound above this frequency and, if it is not filtered out, it is liable to cause distortion at audible frequencies. It appears that nothing of taxonomic significance is lost by such filtering: the ultrasound and audible sound have the same temporal patterns.

After a recording has been made, it needs to be analysed so that it can be compared objectively with other recordings. Our oscillograms are made using an ink-jet recorder which, as the name suggests, squirts a jet of ink at a roll of paper. The machine has two channels, one of which is used for the song, and the other for a timing trace. A typical part of the recording is chosen for analysis, usually at two or three speeds, and then the analyses are filed in a transparent envelope. Back to back with these in the envelope is placed a data sheet, on which all the relevant information about the specimen, recording equipment, conditions etc is typed. These transparent envelopes are kept in a filing cabinet, arranged systematically in major groups, and then alphabetically by genus and species. Because of the full data and analyses that these files contain, they are a very useful data bank in themselves, and can often provide all the information needed on the songs without a tape being taken off the shelf. The museum collection now contains about 3000 recordings on 700 tapes, including some 450 species. About 200 of these are European species with taxonomically useful songs. Throughout the world, it is estimated that, of the 17 000 or so species of Orthoptera, there are about 10 000 with songs that may be useful to the taxonomist.

Specific songs

The classic work on the importance of song in maintaining reproductive isolation was published in 1957 by Perdeck and dealt with three species of common European grasshopper that had presented a taxonomic problem for a century or more. Only one of the three is found in Britain, the Field Grasshopper, *Chorthippus brunneus* (Thunb.). Although very common here, it is much less so on the Continent, where one of the others, *C. biguttulus* (L.), is the most abundant. The third species is *C. mollis* (Charp.). Morphologically, the three are so similar that some entomologists. have considered them to be a single variable species; but the songs are totally different and enable them to be identified at once in the field. Hybrids between these three species are very rarely found in nature, despite the fact that they sometimes occur together, but it is quite easy to produce hybrids in the laboratory. The hybrids are viable and fertile and have intermediate songs and morphology.

Perdeck showed experimentally that the songs of these species were the most important, if not the only, reproductive isolating mechanism. Responsive females make quiet singing movements with their legs when they respond to a male song, and when tape recordings of different songs are played to them they respond only to the song of their own species. This work was carried out in the Netherlands, but the songs had also been described from Germany and it was at that time generally assumed that these three species were found throughout continental Europe. However, Dr Ragge and I have now been able to establish that they are absent from most of the Iberian Peninsula and, apart from *brunneus*, from all but the northernmost part of Italy. They are replaced in these peninsulas by look-alikes with different songs (Ragge, 1987; Ragge & Reynolds, 1988).

Another of the groups in which the songs have helped in clarifying the taxonomy has been the grasshoppers belonging to the European genus *Euchorthippus* Tarbinskii (Ragge & Reynolds, 1984). There were just two species known from the European mainland, *pulvinatus* (Fischer de Waldheim) and *declivus* (Bris.), when Descamps described a third, *chopardi*, from southern France in 1968. He described it purely on morphological grounds, saying that he could find no difference between the songs of the three species. It seemed unlikely that species with the same song could live together as these sometimes do, so we suspected at first that they might be no more than ecological forms of one variable species; the species living in the wettest conditions has short wings and a pointed male abdomen, and the one living in the driest conditions has long wings and a blunt male abdomen. These two are never found together, but both may be found with the third, which lives in intermediate conditions and is intermediate in morphology.

On investigation it was found that there were in fact differences between the songs; careful comparison of the oscillograms showed that the ‘dry’ and ‘wet’ species that are never found together have the most similar songs, but the intermediate species that is often found with either of the other two has a song that is noticeably different, both in the rate of repetition of the chirps and in the structure of the chirps themselves. The two species that never come into contact do not need songs to act as species-isolating mechanisms; their choice of habitat serves that purpose. Thus it was apparent that there really are three valid species, and when our recorded specimens were examined it was found that there were reliable morphological differences between them too. It was surprising to find, however, that the Spanish material, which had been thought to be the ‘wet’ and the ‘intermediate’ species by all previous authors, actually belonged to the ‘intermediate’ and the ‘dry’ species, respectively, and all the taxonomic, ecological and genetic papers of the last 100 years had used the wrong names.

In the next example the study of a song led to the discovery of a new species. The mole-cricket, *Gryllotalpa gryllotalpa* (L.) has a loud song which it produces on warm evenings in late spring and early summer. It is on the verge of extinction in Britain but was causing damage to root vegetables in Southampton gardens a few years ago and is regularly found when the early potatoes are harvested in Guernsey. There appears to be no published record of its song having been heard in the field in Britain since Gilbert White heard it 200 years ago, though Dr Ragge collected insects from the New Forest and tape-recorded the song in captivity in 1968.

Mole-cricket song was being studied in the Dordogne region of France by the physiologist, Dr Henry Bennet-Clark, now of Oxford University. He discovered to his surprise that he heard two different songs, one low pitched, like the British ones, from the damp soil at the bottom of the valley, and the other higher pitched, from the drier soil of the vineyards on the sides of the valley. Those producing the high-pitched song proved to be a new species which he named *vineae* (Bennet-Clark, 1970*a*, *b*). He dug up 20 singing males of each species and found only slight morphological differences between them. He also took plaster casts of their singing burrows and found that these were different too, that of *vineae* being smoother and more regularly shaped. Both have flared openings like the ends of trumpets, which amplify the sound, so that on a quiet night it is claimed that humans can hear the song of *vineae* at a distance of 600 metres.

Among the bush-crickets there are examples of local forms that until now have been regarded as distinct species but that have songs identical to those of species occurring more widely in Europe. In the Decticine genus *Metrioptera* Wesmael the form *buyssoni* (Saulcy) from the Pyrenees has a male calling song identical to that of the widespread species *saussuriana* (Frey-Gessner). These forms are at present regarded as distinct species on the basis of small morphological differences but the identity in song suggests that they would be better treated as conspecific. On the other hand, *caprai* Baccetti from the Apennines has a song that is probably sufficiently different to justify keeping it as a distinct species (Ragge, 1987).

Another example is provided by the genus *Decticus* Serv., in which there is a small short-winged form, *aprutianus* Capra, in the Apennines, which is regarded by Italian authors as specifically distinct from *verrucivorus* (L.), the common Wartbiter. But the songs of the two are identical and it therefore seems likely that only one species is involved (Ragge, 1987).

Although the songs can be used as characters for identification, in the same way as morphological characters, the songs have an added significance. When dealing with closely related species, the best way of discovering how many there are is by using the signals the insects themselves use. It was mentioned earlier that experiments have shown that females often reply to the songs of males of their own species and not to other songs, but some experiments have gone further: they have used artificially generated sounds to test which characteristics of the song are necessary to evoke the female response. Drs Dagmar and Otto von Helversen, working in Erlangen, West Germany, found that in *Chorthippus biguttulus* the legs of a singing male make one big up and down movement followed by two smaller ones, but because the left and right legs are slightly out of phase, the sounds produced by these movements overlap, producing a block of sound separated from the next block by a distinct gap. These experimenters found that females responded best to sounds that did not stray too far from the natural song, and that the important characteristics were that the blocks of sound should be of the right length and separated by silences of the right length. The song changes according to temperature and, as one would expect, so does the response to it (Helversen & Helversen, 1981, 1983).

Conclusion

Unfortunately there have been very few experiments like this, but they appear to show the way in which more accurate taxonomic decisions can be made. They provide the sort of information needed for judging whether populations of the sort recorded in Spain and Italy belong to the same species as those in Northern Europe. The male songs can be analysed and compared to see whether there are clear differences between them that could be recognized by the females. By using the signals that the insects themselves recognize we can be confident that we are dealing with genuine biological species.

ACKNOWLEDGEMENTS

I am grateful to my colleagues Dr D. R. Ragge and Mr W. G. Tremewan for reading the manuscript and making many helpful suggestions.

REFERENCES

Bennet-Clark, H. C. 1970*a*. The mechanism and efficiency of sound production in mole crickets. *J. exp. Biol.* **52**: 619–652.

Bennet-Clark, H. C. 1970*b*. A new French mole cricket, differing in song and morphology from *Gryllotalpa gryllotalpa* L. (Orthoptera: Gryllotalpidae). *Proc. R. ent. Soc. Lond.* (B) **39**: 125–132.

Descamps, M. 1968. Notes sur le genre *Euchorthippus* (Orth. Acrididae). *L'Entomologiste* **38**: 82–87.

Dumortier, B. 1964. Morphology of sound emission apparatus in Arthropoda. In *Acoustic behaviour of animals*. ed. R. G. Busnel, pp. 277–345, Amsterdam: Elsevier.

Helversen, D. von & Helversen, O. von. 1981. Korrespondenz zwischen Gesang und auslösendem Schema bei Feldheuschrecken. *Nova Acta Leopoldina* (N. F.) **54**: 449–462.

Helversen, D von & Helversen, O. von. 1983. Species recognition and acoustic localisation in Acridid grasshoppers: a behavioural approach [pp. 95–107]. In *Neuroethology and behavioural physiology*. eds F. Huber & H. Markl. Berlin: Springer Verlag.

Perdeck, A. C. 1957. *The isolating value of specific song patterns in two sibling species of grasshoppers (Chorthippus brunneus Thunb. and C. biguttulus L.)*. viii +75 pp. Leiden: E. J. Brill.

Ragge, D. R. 1987. Speciation and biogeography of some southern European Orthoptera, as revealed by their songs. In *Evolutionary biology of Orthopteroid insects*. ed B. Baccetti, pp. 418–426. Chichester: Ellis Horwood.

Ragge, D. R. & Reynolds, W. J. 1984. The taxonomy of the western European grasshoppers of the genus *Euchorthippus*, with special reference to their songs (Orthoptera: Acrididae). *Bull. Br. Mus. nat. Hist. (Ent.)* **49**: 103–151.

Ragge, D. R. & Reynolds, W. J. 1988. The songs and taxonomy of the grasshoppers of the *Chorthippus biguttulus* group in the Iberian Peninsula (Orthoptera: Acrididae). *J. nat. Hist.* **22**: 897–929.